

## Evidence From Facial Morphology for Similarity of Asian and African Representatives of *Homo erectus*

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**ABSTRACT** It has been argued that *Homo erectus* is a species confined to Asia. Specialized characters displayed by the Indonesian and Chinese skulls are said to be absent in material from eastern Africa, and individuals from Koobi Fora and Nariokotome are now referred by some workers to *H. ergaster*. This second species is held to be the ancestor from which later human populations are derived. The claim for two taxa is evaluated here with special reference to the facial skeleton. Asian fossils examined include Sangiran 4 and Sangiran 17, several of the Ngandong crania, Gongwangling, and of course the material from Zhoukoudian described by Weidenreich ([1943] *Palaeontol. Sin.* [New Ser. D] 10:1–484). African specimens compared are KNM-ER 3733 and KNM-ER 3883 from Koobi Fora and KNM-WT 15000 from Nariokotome. Hominid 9 from Olduvai is useful only insofar as the brows and interorbital pillar are preserved.

Neither detailed anatomical comparisons nor measurements bring to light any consistent patterns in facial morphology which set the African hominids apart from Asian *H. erectus*. Faces of the African individuals do tend to be high and less broad across the orbits. Both of the Koobi Fora crania but not KNM-WT 15000 have nasal bones that are narrow superiorly, while the piriform aperture is relatively wide. In many other characters, including contour of the supraorbital torus, glabellar prominence, nasal bridge dimensions, internasal keeling, anatomy of the nasal sill and floor, development of the canine jugum, orientation of the zygomaticoalveolar pillar, rounding of the anterolateral surface of the cheek, formation of a malar tubercle, and palatal rugosity, there is variation among individuals from localities within the major geographic provinces. Here it is not possible to identify features that are unique to either the Asian or African assemblages. Additional traits such as a forward sloping “crista nasalis,” presence of a “sulcus maxillaris,” a high (and massive) cheek coupled with some flexion of the malar pillar, and a posterior position for the incisive canal are present in all groups. These characters seem to be plesiomorphic, in comparison to the derived states evolved in later humans.

Much or all of the variation in facial form can be attributed to sex dimorphism and/or local differentiation of populations within the Asian and African geographic regions. Metric differences among the fossils are comparable to those documented in a subset of recent *H. sapiens*, and there is no

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evidence that the Pleistocene specimens show greater dispersion than expected within a single species. This finding is generally in keeping with observations made on other parts of the cranium, lower jaw, and teeth. All of the hominids can be placed in *H. erectus*. Although its phylogenetic origins remain obscure, this lineage must be rooted in Africa. The species flourished for a long time. At several sites in China, *H. erectus* is known from deposits of the later Middle Pleistocene, while at Ngandong in Indonesia, archaic people may have survived even into the Late Pleistocene (Swisher et al. [1996] *Science* 274:1870–1874). The Ngandong fossils may record the last appearance of the lineage. *Am J Phys Anthropol* 106:61–85, 1998. © 1998 Wiley-Liss, Inc.

The first fossils to be attributed to the species now called *Homo erectus* were discovered in Java, late in the last century. Eugene Dubois's excavations at Trinil brought to light a skullcap and later a complete femur, and it was on the strength of these finds that Dubois named his new species in 1894. More evidence came from the cave of Zhoukoudian in China, and for more than half a century, *H. erectus* was known exclusively from the Far East. Only after intensive fieldwork in lake deposits at Ternifine in Algeria produced three mandibles, a parietal, and teeth in 1954 and 1955 was it widely recognized that this species had lived in Africa as well as Asia. Arambourg's (1963) descriptions of the Ternifine (now Tighenif) jaws showed numerous similarities to the specimens from Zhoukoudian. At about the same time, pieces of a braincase were recovered at Olduvai Gorge in Tanzania. Given its heavy supraorbital torus, low and constricted frontal and flexed occiput, this individual (OH 9) could be compared favorably to the skulls already on record from China and Indonesia. Later in the 1970s, a wealth of material including several crania, mandibles with teeth, and even portions of an articulated skeleton were collected in the Turkana Basin of northern Kenya. Also, it became clear that some of the African fossils were very ancient, suggesting that *H. erectus* could have evolved in this region and then spread to other parts of the Old World.

This interpretation was challenged in the 1980s, by workers who argued that the Asian specimens present autapomorphic features. Frontal keeling, an angular torus on the parietal, some characters of the tempo-

ral bone, and overall thickening of the vault, said to be expressed in the Far Eastern crania but absent in African individuals, were taken by Andrews (1984) to mean that two species should be recognized and that *H. erectus* must be restricted geographically to Asia. Tattersall (1986), Bilsborough and Wood (1988), Groves (1989), and Wood (1991) generally agree with this position. Wood (1994) admits the possibility of some migration of Dubois's taxon into eastern Africa, as demonstrated by OH 9 from Olduvai, but this species is cast as an evolutionary side branch, peripheral to the mainstream of human evolution. The remains from Koobi Fora are more likely to represent a population directly ancestral to later humans. Wood (1994) now refers the fossils from the Turkana Basin to *H. ergaster*, while Clarke (1990, 1994) holds that all the African specimens, including OH 9, can be attributed to *H. leakeyi*.

Other authors such as Rightmire (1986, 1990), Kennedy (1991), Bräuer and Mbua (1992), Harrison (1993), Kramer (1993), and Bräuer (1994) have maintained that differences between the Far Eastern and African hominids are slight, and that all can be grouped together as one species. Just what paleontologists mean by the term species is not always clear. Different concepts are in use, and not all workers are careful to spell out their thinking on this point. Consequently, there is some confusion, but the *H. erectus* controversy does not reduce simply to a choice of which concept is preferred. A key question is whether there are consistent differences in anatomy among the fossils, or whether the variation observed is compar-

actively minor. Here I address the issue of species recognition in a limited way, but my main goal is to present evidence from the facial skeleton which suggests similarities between the Asian and early African assemblages. This evidence does not support any partitioning of the *H. erectus* hypodigm into distinct components on the basis of geography.

## MATERIALS AND METHODS

My research emphasizes the utility of facial characters to the sorting process and more generally to the assessment of relationships among taxa of Pleistocene humans. The faces of ancient hominids exhibit much variation in supraorbital anatomy, structure of the orbits, cheek and nasal region, and shape of the maxillary alveolar process. Often the factors underlying this variation are poorly understood, but some suggestions concerning function are reasonable. The protruding nose of *H. erectus* may be related to increasing volume of the nasal cavity and the capacity to retain moisture (Franciscus and Trinkaus, 1988). The nose and midface may also participate in a heat exchange mechanism for cooling venous blood and regulating brain temperature (Dean, 1988). Biomechanical considerations help to explain patterns of robusticity and buttressing, positioning of the masticatory muscles, and changes in the dental arcade as a consequence of stress generated by loading of the teeth and jaws. Whatever their functional basis, anatomical complexes of this sort have been molded by natural selection, and the face should provide information that is useful to taxonomy. Such findings are best interpreted within the context provided by other studies of the braincase, cranial base, mandible, and dentition.

Here the face is defined broadly to include the supraorbital structures and glabella but not other parts of the frontal bone. Special attention is given to aspects of supraorbital anatomy, orientation of the orbit and zygomatic arch, and shape of the nasal bridge, piriform aperture, subnasal region, and hard palate. Tooth crowns and roots are not treated in detail, and the lower jaw is not considered. Crania for which some or all of the facial skeleton is preserved are known

from Asia and from eastern Africa. Only those specimens providing at least some insight into the expression of important features are listed below. With the exception of the Zhoukoudian hominids, all of the fossils examined are the originals, stored in Frankfurt, Bandung, Yogyakarta, Beijing, Nairobi, and Dar es Salaam.

### Asian *Homo erectus*

In Java, several crania have been recovered from sediments accumulated within the Sangiran dome, and the most complete is Sangiran 17. Much of the face is intact, including the supraorbital structures, nasal saddle, outline of the right orbit, and parts of the cheek and palate. Recently, casts have been used by Aziz et al. (1996) to prepare a new reconstruction, which helps to clear up some of the problems apparent in the orientation of the facial skeleton. Observations and measurements taken on both the original fossils and the reconstruction are reported here. Sangiran 4 is represented by portions of the maxillae contributing to the floor of the nose and the hard palate, while Sangiran 10 retains a little of the orbital margin and a left zygomatic bone, not attached to the rest of the cranium.

Another important site is Ngandong, also in central Java. Unfortunately, the skulls from Ngandong are broken, and facial bones have been lost in all cases. Because of their condition, these hominids are not central to my research program. Nevertheless, for several of the specimens, the supraorbital tori are at least partially intact, and the interorbital region can be studied.

In China, excavations at Zhoukoudian produced a number of *H. erectus* bones in the 1920s and 1930s. As is well known, nearly the entire collection of fossils from Locality 1 disappeared in 1941, but Weidenreich's (1943) descriptions of the crania are richly detailed, and good casts have survived. For Skull II and Skull V (the 1966 original), some information can be obtained from the supraorbital region and the nasal root. Skull X is more complete. Not only the brow but also a maxilla and left zygomatic bone are present. Skull XI is one of the finest of the Zhoukoudian specimens. It was found in pieces, but many of these could be fitted

together without difficulty. The upper aspect of the nasal bridge is damaged, but the left maxilla is available. This individual is the basis for Weidenreich's reconstruction of a complete female cranium. The restored face is subject to the concerns associated with any composite of this sort, but it is useful for comparisons. For Skull XII, almost the entire frontal bone is preserved, along with its contacts to the nasal saddle and the cheek. The outline of the left orbit is partially complete. Taking this presumed male cranium as a guide, Tattersall and Sawyer (1996) have recently executed a new reconstruction. In this face, some of the questionable features displayed by Weidenreich's female have been modified.

Gongwangling is situated near the city of Lantian in northwestern China. Facial pieces associated with the Gongwangling cranium include the nasal root and bridge, the left maxillary frontal process, and the subnasal region. Also, the supraorbital structures can be examined, although the entire frontal bone has been subject to much crushing and distortion.

#### Material from Africa

Prospecting in the Koobi Fora region, east of Lake Turkana in Kenya, has resulted in the recovery of two crania, described variously as early *H. erectus*, *H. ergaster*, or *H. leakeyi*. The face of KNM-ER 3733 is quite complete. The brows, nasal bridge and piriform aperture, zygomatic bones, and palate are in relatively good condition, and overall accuracy of the reconstruction is not in question. The face is attached securely to the braincase. KNM-ER 3883 is less well preserved. The supraorbital region, interorbital pillar, parts of both nasals, and the right cheek are present, so the orbit and lateral wall of the nasal aperture can be studied on one side. Other specimens from Koobi Fora are less informative. Several probably document individuals similar to KNM-ER 3733, but even for KNM-ER 730, which offers a little of the brow and a fragment of maxilla, few facial features are revealed.

Nariokotome on the west side of Lake Turkana is well known as the site where most of a subadult skeleton was recovered in

the 1980s. The skull of KNM-WT 15000 has been pieced together from many fragments. The process of aligning the maxillae, setting the face to the braincase, and other aspects of the reconstructive effort are described by Walker and Leakey (1993). Much of the supraorbital architecture and the glabellar prominence are missing, but the upper parts of both nasal bones, the maxillae, and the cheeks are present, and all of the teeth have been glued back into position. Although slight plastic deformation remains, this is an important specimen, throwing light on growth of the facial skeleton and braincase (Richtsmeier and Walker, 1993).

For Hominid 9 from Olduvai Gorge, little of the face is preserved. Nevertheless, the brow is intact, as is much of the interorbital pillar. In these features (as in many additional aspects of cranial anatomy), OH 9 can be compared to Sangiran 17, the Ngandong assemblage, and several of the Zhoukoudian individuals.

#### Anatomical traits

For each of the more intact specimens, overall form of the supraorbital region is described. Any special thickening is noted, along with the condition of glabella and the relation of this prominence to the tori and to nasion below. The course followed by the nasofrontal and frontomaxillary sutures, the proportions of the individual nasal bones, and the shape of the saddle (including any midline keeling) are recorded. In side view, the relationship of the lateral margin of the aperture [the "crista nasalis" of Weidenreich (1943)] to the floor of the nose is assessed. In the Zhoukoudian face, this crest carries the lower edge of the aperture forward, whereas in modern humans it is more vertical.

Aspects of subnasal morphology to be checked include the presence of lateral and/or spinal crests [terminology of McCollum et al. (1993)] and any conspicuous anterior nasal spine. In place of the latter, many archaic hominids have just a small tubercle marking the most forward attachment of the septum. The topography of the nasal floor may be smooth or stepped. Also from the front, the lateral boundary of the aperture is scored as rounded or relatively sharp. The development of any canine jugum is noted,

as is the extent to which this pillar reaches superiorly. Lateral to the jugum, there may be a furrow-like sulcus rather than a broader "canine fossa" situated above the premolar roots. Such a sulcus is expressed in the Zhoukoudian specimens. The orientation of the zygomatic process of the maxilla, the form of the malar incisure, the shape of the cheek itself, and the presence of any distinct tubercle are recorded. The malar tubercle occupying the lower anterior aspect of the zygomatic bone may be knob-like or inferiorly projecting. Its relation to the masseter origin is variable (cf. Pope, 1991).

The shape of the hard palate and the degree of anterior flexion are noted. The condition of the palatal surface is scored as rugose or smooth. The positioning of the entrance to the incisive canal is an important attribute. This opening tends to be in a relatively posterior location in Chinese *H. erectus*, and the course taken by the canal is inclined relative to the alveolar plane (Weidenreich, 1943). In recent humans, the foramen opens directly behind the incisor roots, and the canal is more nearly vertical.

### Metric approaches

Measurements are listed in Table 1. Nasal bridge dimensions follow Weidenreich (1943), while other measurements are defined by Howells (1973), Rightmire (1975), and Bilsborough and Wood (1988). Some register aspects of robusticity, while others can be used to assess proportions of the facial skeleton. A number of breadths are included, along with the corresponding subtenses taken at nasion, the nasal saddle, and other points in the midline. These permit calculation of angles quantifying projection of the nose or subnasal region in the transverse plane.

Specimens are compared in ratio diagrams. For each variate, a horizontal scale records differences among one or more fossils, relative to an individual (or group) taken as a standard. All dimensions are first converted to logarithms. Distances between values plotted on each horizontal scale are proportional to the ratios of the original measurements. Therefore, any specimen having proportions similar to the standard

TABLE 1. Measurements of the facial skeleton

1. Supraorbital torus thickness. Measured both at the center of the orbit and laterally, near the zygomaticofrontal boundary.
2. Nasion-prosthion length.
3. Biorbital chord. Upper facial width, taken at the most anterior points on the zygomaticofrontal sutures.
4. Nasion subtense. To nasion from the biorbital chord.
5. Nasion angle. Calculated from the subtense (4) and one half the biorbital chord (3). NFA of Howells (1973).
6. Width of nasal bridge. Measured at the anterior lacrimal crests, following Weidenreich (1943).
7. Nasal bridge height. Taken as a subtense to nasion, from the chord defined as (6).
8. Nasal bridge index. The ratio of height to width, as used by Weidenreich (1943).
9. Nasal bridge angle. Projection of nasion relative to the anterior lacrimal crests, calculated from the subtense (7) and one half the width (6).
10. Orbit breadth. From dacryon to ectoconchion.
11. Orbit height. Taken between the upper and lower margins, approximately at the center of the orbit and perpendicular to its long axis.
12. Midorbital chord. The distance between the two zygoorbitalia.
13. Naso-orbital subtense. Taken to the deepest point in the nasal profile, using the midorbital chord as a baseline.
14. Naso-orbital angle. Projection of the nasal saddle relative to the lower orbital margins, calculated from the subtense (13) and one half the chord (12).
15. Nasal breadth. Taken as a maximum between the anterior edges of the aperture.
16. Nasal height. From nasion to the lowest point on the inferior margin of the aperture, on either side.
17. Nasoalveolar clivus length. Nasospinale to prosthion.
18. Bimaxillary chord. Taken between the points where the zygomaxillary suture intersects the line of masseter origin.
19. Subspinale subtense. To subspinale from the bimaxillary chord.
20. Angle at subspinale. Calculated from the subtense (19) and one half the chord (18).
21. Prosthion subtense. To prosthion from the bimaxillary chord.
22. Angle at prosthion. Calculated from the subtense (21) and one half the chord (18).
23. Cheek height. Measured as a minimum, from the inferior border of the orbit to the lower margin of the maxilla.
24. Maximum malar height. Taken approximately vertically, from the inferior margin of the malar surface to the tip of the frontal process.
25. Palate breadth. Measured internally between the margins of the alveoli, at the level of the M<sup>2</sup>s.
26. Palate length. Measured internally from orale to staphylion.

will be represented in the diagram by a series of points which, when connected, fall approximately parallel to the vertical zero axis. The plot for a differently shaped face will consist of points which are not all equidistant from this axis.





Fig. 1. Facial and lateral views of Sangiran 17. The facial skeleton of this individual is more complete than in other specimens from Java. Despite damage to the nasal root and the maxillae, several of the features characteristic of *H. erectus* are preserved, including a relatively long nasoalveolar clivus, a channel-like maxillary sulcus, and a very massive cheek.

#### ANATOMICAL DESCRIPTIONS

Here it is appropriate to treat several of the more important hominids from Asia and Africa in substantial detail. Among the Indonesian representatives of *H. erectus*, Sangiran 17 possesses the best face available for study. Any investigation of the morphology characteristic of Dubois's species must draw heavily on the Sangiran material and on the remains from Zhoukoudian in China. For the latter, Weidenreich's (1943) monograph supplies much information. It is unnecessary to reiterate Weidenreich's accounts for each of the facial bones, but on many points I have summarized his findings and used these as a benchmark for comparisons. Descriptions of the Indonesian and Chinese fossils provide the basis for identifying similarities linking the Asian and African assemblages, or differences that may set some or all of the African crania apart. For eastern Africa, the main specimens are KNM-ER 3733 from Koobi Fora and KNM-WT 15000 from Nariokotome. In both cases, nearly all of the face is present.

#### Sangiran 17

The face of Sangiran 17 is somewhat damaged. On the right, the supraorbital torus is separated slightly from the glabellar region by a vertical crack, which extends posteriorly into the frontal squama (Fig. 1). The surface just above glabella is intact, but below this point, bone is missing from an irregular break, now filled with reconstructive material. The nasal root and interorbital pillar have been displaced upward. The supraorbital tori are thick, both centrally (17 mm) and laterally (13 mm). These structures are similar in form to those of the larger Ngandong crania. There is a resemblance also to OH 9, although the Sangiran tori are not so massive as in the African individual. The supratatorial surface is depressed near the midline, and glabella protrudes, when damage to this area is corrected in the reconstruction of Aziz et al. (1996).

Sutures adjacent to the nasal root are largely obliterated. The position of nasion can be estimated, and here the combined

width of the nasal bones is at least 13 mm. These bones appear to broaden below (but both are broken). Keeling in the midline is pronounced. To either side, the nasal elements are flattened, so as to give the saddle a distinctly "tented" shape. On the left, the anterior lacrimal crest can be located. At this level the width of the nasal bridge is approximately 24 mm, and an estimate for the subtense taken from this chord to nasion is 9 mm. The bridge height/width index of 37.5 is almost identical to that for Zhoukoudian Skull XII, but a little greater than the index of 30.0 obtained for the Skull XI reconstruction.

In side view, the nasal profile of Sangiran 17 is concave throughout its length. It is unlikely that this contour is much affected by bone missing from the nasal tips. Relatively more of the lateral wall of the nose is present on the right. Unfortunately, this border is interrupted by a break passing transversely through the maxilla, and there are signs of crushing along the lower orbital margin and at the infraorbital foramen. The full length of the aperture is not preserved. Nevertheless, it is apparent that the "crista nasalis" must slope forward to merge with the nasal floor at a point well anterior to rhinion. The part of the crest that is intact is straight, rather than curved as is usually the case for later *H. sapiens*.

The subnasal aspects of the maxillae are eroded, especially on the left where much of the cortex has been broken to reveal pockets of cancellous tissue encrusted with a few remaining grains of matrix. Where the clivus is undamaged, this surface passes without interruption into the floor of the nose. At the midline, there is a slight prominence. This structure does not seem to have reached posteriorly along the nasal sill, nor does it project forward like the spine of recent humans. Laterally, the nasal floor is gently hollowed. There is no evidence for any transverse cresting. The back of the sill is less well preserved. Here several small plates of bone have been thrust downward, so as to obscure the region where the incisive fossa should be situated. There is no indication of any change in elevation of the nasal surface, but whether this topography should be scored

as smooth rather than stepped in the terminology of McCollum et al. (1993) is unclear, because of the poor condition of the hard palate.

Because the maxillary alveolar processes are damaged, and sockets for the incisors have been lost, prosthion cannot be located at all accurately. A minimum estimate for length of the clivus is 25 mm, but in the reconstruction of Aziz et al. (1996) this distance is increased to 28 mm. Enough of the contour is preserved to suggest some convexity, relative to the adjacent canine root. The canine is in place on the right side. Some of the alveolar bone surrounding the root is missing, but it is clear that the jugum could not have been prominent. This structure does not reach upward toward the margin of the nose. Posteriorly, at about the position of P<sup>3</sup>, the surface of the maxilla is hollowed. This depression is restricted in extent and channel-like, trending superiorly toward the infraorbital foramen. The channel may terminate below the foramen, but cracks and pieces of displaced cortex obscure its exact course. There is more damage laterally, but this region does not exhibit any of the generalized hollowing that would be termed a canine fossa.

The cheek is very massive. Distance from the orbital margin to the masseter origin is 39 mm, while minimum height measured on the maxilla is 37 mm. Swelling of the anterolateral aspect of the zygomatic bone gives the entire cheek a rounded appearance, lacking any strong degree of angulation. Protrusion of the surface at or just above the roughened masseter attachment is especially pronounced. In the original (but less so in the reconstruction), the malar face slopes laterally, so as to accentuate the bizygomatic breadth. The latter can be estimated only by reference to the midline but must substantially exceed the biorbital diameter.

The blunt and rugged zygomaticoalveolar pillar originates above M<sup>1</sup>/M<sup>2</sup>. This strut is nearly horizontal in orientation, but to some extent its root must be affected by a zone of breakage which extends obliquely downward from the infraorbital foramen. Although the incisure is rather strongly flexed,

this curvature has been exaggerated in the reconstructed face. A malar tubercle, partly eroded, is associated with the anterior-most extent of the masseter attachment. This irregular prominence projects inferiorly at the approximate position of the zygomaxillary junction.

Neither length nor breadth of the hard palate can be determined with certainty, but it is relatively long, narrow, and shallow. In contrast to the condition described for the Zhoukoudian hominids by Weidenreich, most of the ridges and small depressions which characterize modern humans are not apparent on Sangiran 17. A point of similarity to the Chinese specimens is that the opening to the incisive canal is situated rather far posteriorly. The canal itself seems to follow an oblique path upward toward the nose.

#### Sangiran 4

The maxillae of this famous individual are broken, but the nasal floor, the intermaxillary crest, and parts of both sinuses are preserved. On the right side, the lower aspect of the sinus is intact, and this cavity extends forward to a point just behind the canine root. Its inferior surface lies well below the level of the nose, as in the Zhoukoudian face. The nasoalveolar clivus is largely complete, although bone is missing from the incisor alveoli, and all four incisors have been lost. To the left of the midline, there is a crack reaching from the central incisor socket upward toward the margin of the nasal aperture. As noted by Weidenreich (1945), part of the jaw lateral to this break has been displaced slightly, but any loss of bone and consequent narrowing of the palate cannot be substantial. The alveolar process is cracked at P<sup>3</sup>/P<sup>4</sup>, and the P<sup>4</sup> has been partially displaced from its socket. Although the palatal surface has sustained some crushing, deformation of the specimen cannot be nearly so extreme as claimed by Krantz (1994).

In the nasal region, several important features are revealed. It is clear that the incisive crest projects anteriorly to form a spinous process. This process is elevated and still quite prominent, despite damage to its tip. Spinal crests (cf. McCollum et al., 1993) passing laterally from it are eroded

and now resemble roughened lines marking the forward boundary of the nose. Three or 4 mm posteriorly, there is a second set of (very faint) transverse crests. Although a little of the wall of the left cheek is present, crushing prevents any determination of the relationship between cresting on the nasal sill and the lateral margin of the piriform aperture. Inside the cavity, the floor is essentially intact on one side, and here there is no change in relief between the sill itself and the surface posterior to the incisive fossa. Thus the entrance to the nose is smooth, not stepped. Insertion of the vomer seems to be "high" relative to the anterior nasal spine, as in recent humans (see McCollum et al., 1993).

Height of the clivus as measured from nasospinale to prosthion is 29 mm, while distance from the anterior spine to the lowest point between the central incisor sockets is 34 mm. Insofar as can be ascertained, the subnasal surface is gently convex in the sagittal plane. Reconstruction of this contour is complicated by the fact that the incisor alveoli are broken, but here Sangiran 4 must be similar to the Zhoukoudian condition. The prominent precanine diastemata have elicited much prior comment. The canines themselves are large-crowned teeth, but there is little swelling of the bone associated with their roots. The juga are only slightly developed. On the left where more of the maxillary wall is preserved, it is apparent that no pillar could have reached upward to thicken the margin of the nose. As the cheek region is missing, nothing can be said concerning either the furrow characteristic of Chinese *H. erectus* or any canine fossa.

Much of the hard palate is complete, if somewhat damaged. The entrance to the incisive canal has been broken, but this opening is well removed from the front of the jaw. The distance from a line tangent to the borders of the incisor sockets to the anterior margin of the fossa is approximately 10 mm. Inclination of the axis of the canal relative to the alveolar plane must be comparable to that observed in the Zhoukoudian specimens. The palatal surface has been described by Weidenreich (1943) as less rugged than is usual for later *Homo*, but in fact



small grooves and crevices are present. There is a general resemblance to Sangiran 17.

### Gongwangling

The Gongwangling frontal has been subjected to crushing, involving both the squama and the supraorbital structures. On the left side, it is apparent that the brow is curved slightly, to produce an arch that is highest over the center of the orbit. Here the torus is quite thick (>15 mm), and it does not thin appreciably prior to joining the zygomatic bone. Glabella would likely have been set in a shallow depression. Just above this landmark, the surface of the frontal is flattened, but laterally there is more supratoral hollowing. This "sulcus" could not have been so pronounced as in the Zhoukoudian individuals.

The interorbital region is massively constructed. Suture detail is partly obliterated, but the frontomaxillary and nasofrontal sutures seem to follow a straight course, coming to a peak just at nasion. The anterior lacrimal crest can be located (tentatively) only on the left side. If some allowance is made for distortion on the right, width of the nasal bridge can be estimated as 24 mm, and the subtense to nasion is approximately 8 mm. The resulting nasal bridge index is 33.3. Only the upper segments of the nasal bones remain in place. Their combined width is 13 mm superiorly, and there is some indication of broadening below. An internal nasal keel is quite distinct.

Neither the roof nor any of the lateral margin of the piriform opening has survived. Also, there is no contact between the bone of the infraorbital region and the jaw below. On separate maxillary fragments, some of the nasal sill is present, but this surface exhibits pitting and is clearly eroded. There is a small central spine, no longer prominent. From its apex, faint ridges pass for a short distance to either side, but these transverse crests do not approach the borders of the nose. They do constitute a boundary demarcating the floor of the cavity from the subnasal portion of the jaw.

The clivus itself is incomplete. Its superior aspect drops sharply downward to terminate in a rough break passing through the sockets for the anterior teeth. Here there are

moderately deep vertical corrugations associated with the incisor alveoli. Otherwise, this surface is flattened. Wu and Poirier (1995) suggest that this flattening is a consequence of deformation. Certainly there are indications of damage, but the original contour could not have been so strongly convex as in Woo's (1966) reconstruction. There is substantially less prognathism than is characteristic of Zhoukoudian Skull XI. Form of the clivus seems more comparable to that of Skull XII [as illustrated by Tattersall and Sawyer (1996)] and some of the African specimens.

On the right, a good deal of the canine jugum is intact. This swelling is prominent and extends upward, apparently to merge with the nasal margin. The degree to which the border itself may have been rounded superiorly can no longer be ascertained. Behind the jugum, there are traces of a vertical furrow. Such a sulcus, rather than a more open canine fossa, seems to be the norm for Asian *H. erectus*. Only a little of the zygomaticoalveolar pillar is preserved, immediately above the position of M<sup>1</sup>. This structure is broken laterally, and the shape of the incisure is largely indeterminate.

### KNM-ER 3733

The supraorbital tori of KNM-ER 3733 are a little heavier laterally (9 mm) than at the center of the orbit (8 mm), but are otherwise quite uniform in thickness. Glabella is less massive than in some of the larger African and Asian crania, and nasion is only moderately recessed (Fig. 2). The nasal bones are nearly complete. The nasofrontal and frontomaxillary sutures follow essentially a horizontal course, but the left nasal is 1 or 2 mm higher than its companion, and here there is minor asymmetry. At the suture line, these elements together are 8 mm wide. Inferiorly, the bones fan out to a width of about 18 mm. Lateral length cannot be measured accurately, but on the left side this must be at least 27 mm.

Apart from slight midline keeling, the nasal bridge is rounded in transverse section. The nasal bones and adjacent portions of the maxillae are set in an irregular curve, although this arch is not very high. Width of the bridge as measured from the anterior



Fig. 2. Facial and lateral views of KNM-ER 3733 from Koobi Fora. Although the maxillae are incomplete, other parts of the face are in good condition. Upper facial width is a little less in this individual than in others from Zhoukoudian or Sangiran, but there are numerous resemblances to *H. erectus* as known from the Far East.

lacrimal crests is 22 mm. Height taken as a subtense must be about 8 mm, so the height/breadth index is very close to the figure given by Weidenreich for Skull XII from Zhoukoudian. From the side, the nasal profile is concave over about two thirds of its length, but the lower extremities of the bones bend downward. This interruption of the curvature is slight but seems to reflect anatomical reality, and here there is some contrast to the description provided by Weidenreich (1943) for the Chinese fossils. On the left, enough of the maxilla is preserved to show that the lateral margin of the nose slopes forward as it passes inferiorly to merge with the nasal floor. The "crista nasalis" is neither deeply concave nor vertical as it tends to be in modern crania, but instead carries the lower edge of the aperture anteriorly, relative to the overhanging roof. In this character, KNM-ER 3733 resembles the Zhoukoudian condition.

In facial view, the upper aspect of the clivus grades evenly into the floor of the nose. Just where the maxillae meet at the midline, there is a low ridge, partly eroded. This incisive crest seems to reach to the

front of the sill but is nowhere prominent. It is unlikely that a (true) spine would have been developed. On the right, where some of the original surface is present, there is no sign of any transverse crest anteriorly. Here the sill is gently concave from side to side, and it appears to join smoothly with the lateral border of the aperture. At the posterior boundary of the alveolar process, there is some blunt cresting adjacent to the incisive fossa. This spinal crest is intact for only a short distance. Behind it, the nasal floor slopes sharply downward. This change in relief is evident near the midline and also laterally, so the topography of the nasal entrance is stepped in the terminology of McCollum et al. (1993). The level of the vomer insertion cannot be determined.

Below the nose, the maxillary alveolar process is badly eroded. All of the anterior teeth have been lost, and their sockets are damaged, especially labially where large areas of bone are missing. Nevertheless, it can be established that this subnasal surface of the jaw is flattened. Even if the tooth roots and surrounding structures were intact, the clivus would not exhibit any appre-

cial central convexity. Here there is definite contrast to the *H. erectus* female from Zhoukoudian.

On the right side, where the lateral part of the clivus and more of the alveolar process are preserved, a canine jugum is well developed. This rounded swelling extends upward to a point several millimeters below the nasal floor, where it is broken away. On the left, little of the actual jugum has survived, but some of the maxillary wall is present, and the lower part of the nasal margin is thickened. This thickening decreases superiorly, where the "crista nasalis" is quite thin. The degree to which this plate of bone may be everted is difficult to assess, because of damage to the specimen.

The zygomatic process of the maxilla is missing on both sides. On the right, there are traces of a shallow groove, passing downward toward the broken roots of the premolars. Whether this entire fossa was furrow-like as in the Asian fossils, or more expanded as in recent humans, cannot be determined. The surface of the zygomaticoalveolar crest is badly eroded (just a few small plates of cortex are in place above the M<sup>1</sup> roots), so the shape of the malar incisure is also uncertain. The cheek itself is relatively heavily constructed. The distance between the infraorbital margin and the masseter attachment is about 33 mm, while the minimum height measured on the maxilla is 34 mm. The external surface of the cheek is flattened, but there is a malar tubercle. This feature is best expressed on the right, where a little of the zygomaxillary junction seems to be present. It occupies the lower anterior aspect of the zygomatic bone and probably projected downward, just at the suture. So far as it is preserved, this tubercle is similar to that described for the Zhoukoudian hominids by Weidenreich.

The hard palate is rectangular in outline, highly arched, and relatively narrow (Leakey and Walker, 1985). Although there is damage to the incisor sockets, some of the anterior-most part of the alveolar process has survived. It is clear that the palatal opening to the incisive canal lies 8–10 mm behind the alveolar margin, as in *H. erectus* from the Far East. Some of the canal has been obliterated, but the groove that remains

passes obliquely upward and posteriorly, toward the nasal floor. In its generally rugged appearance, the surface of the KNM-ER 3733 palate resembles that of both the Zhoukoudian specimens and later people.

#### KNM-ER 3883

The glabellar prominence of this individual displays numerous cracks, some of which have spread and filled with matrix. Similar damage has affected the interorbital pillar. Nevertheless, the upper parts of both nasal bones are in place, and these are positioned slightly more superiorly relative to the maxillary frontal processes than is true for KNM-ER 3733. At the suture line, the nasal bones have a combined width of about 7 mm. They expand rapidly to a width of 16 mm, but the lower extremities are missing. Lateral length can be estimated only by reference to the adjacent maxillary wall, preserved on the right side. Probably the nasal bones were comparable in size to those of the other Koobi Fora cranium. Width of the nasal bridge is roughly 22 mm. Crushing has somewhat altered the shape of the cross section, and height of the bridge cannot be measured very accurately. An estimate for the subtense (relative to the anterior lacrimal crests) is 9 mm, and this yields a simple height/breadth ratio of 40.9. The bridge is evenly rounded, and there is no ridge or keeling in the midline. In side view, the saddle is concave.

The cheek is incomplete. Even on the right side, the anterior part of the zygomatic bone is broken, and much of the maxilla is missing. Insofar as its dimensions can be reconstructed, the cheek is larger than that of KNM-ER 3733. The oblique distance from the orbital rim to the masseter attachment must be about 39 mm. This malar surface is strongly convex, and probably the region adjacent to the zygomaxillary suture was rounded and very prominent. This is the case for Asian *H. erectus* in which the corresponding facial parts are present, as exemplified by Sangiran 17. Whether a distinct malar tubercle was expressed cannot be ascertained. More medially, the plate of bone contributing to the inferior orbital margin and the wall of the nose is gently concave,

but there is no indication that a canine fossa was developed.

#### KNM-WT 15000

Apart from the glabellar region, brows, and interorbital pillar, the face of this young individual is quite well preserved. The nasofrontal and frontomaxillary margins together describe a low arc. At the suture line, combined width of the nasal bones is 17 mm. Both elements are broken inferiorly, but it is clear that they would have expanded slightly over the aperture. The difference between least and greatest breadths is small, compared to the condition evident in the Koobi Fora crania. On the right, lateral length may have reached 27 mm. Width of the nasal bridge is 32 mm, while height taken as a subtense is 9.5 mm. The bridge index is thus 29.6. As with KNM-ER 3883, this structure is rounded in cross section, and no keel is present. What remains of the saddle is concave in profile.

The bone outlining the nasal aperture is everted superiorly, near the nasomaxillary junction. Lower down, this edge is thickened but would still be characterized as "sharp" by the criteria of McCollum et al. (1993). The "crista nasalis" curves forward throughout its entire length, so as to meet the nasal floor at a point well in advance of rhinion (the position of which can be estimated). The slope of this midfacial profile seems more pronounced than in KNM-ER 3733 and closely matches that of the Chinese specimens described by Weidenreich (1943). Such morphology is in keeping with the orientation of the clivus, which is long and projecting. The subnasal surface is relatively flat. There are faint vertical corrugations associated with the incisor roots, but these do not produce much convexity in the transverse plane. Canine juga are poorly developed, but in an adult these might serve to "square off" the jaw, as in KNM-ER 3733.

The piriform aperture is broad and slightly higher than that of the Koobi Fora cranium. An incisive crest is prominent. This longitudinal ridge, bifurcated at the intermaxillary suture, projects far enough anteriorly to be visible from the side, although it does not clearly form a spinous process. To either side, the nasal sill is contoured as a smooth

gutter. These surfaces are marked only by faint transverse crests originating at the midline and merging with the wall of the nose several millimeters posterior to its lateral margins. Behind these spinal crests, the nasal floor slopes downward. There is no abrupt step, either centrally at the incisive fossa or toward the side. The entrance to the cavity must be scored as smooth. Here much of the intermaxillary crest has been broken away, but the section remaining suggests that the insertion of the vomer was "intermediate" or "high" (McCollum et al., 1993), so as to ensure some contact with the nasal sill.

From the nasal opening, the maxillary walls recede toward large infraorbital foramina, set 9–10 mm below the orbital margins. Each foramen opens downward into a palpable furrow, which serves to demarcate the body of the maxilla from its zygomatic process. In the KNM-WT 15000 boy, these vertical furrows are not very pronounced. But as the permanent canines erupted and their juga were expanded, the channels would probably have become a little deeper. Such morphology is characteristic of Asian *H. erectus*. Laterally, the anterior-facing portion of the zygomatic process is quite flat. There is no generalized hollowing corresponding to the canine fossa of later humans.

The cheek is already rather massive. Height taken on the maxilla, avoiding the masseter attachment, is 30 mm. The inferior orbital rim is blunt, and below it the surface is gently rounded. At this stage of the growth process, there is little indication of the swelling likely exhibited by the KNM-ER 3883 adult. The area of masseter origin seems quite extensive, reaching to or across the zygomaxillary suture. Neither at the suture itself nor elsewhere on this aspect of the cheek is any tubercle developed. Inferiorly, the root of the zygomatic process is greatly thickened. This pillar arises above P<sup>4</sup>/M<sup>1</sup> and curves laterally to become almost horizontal. There is clear expression of an incisure, and this flexion could have become more pronounced, as rugosity of the masseter attachment increased with age.

Along with the alveolar process and some of the maxillary sinus on the right side, much of the hard palate is preserved. The



latter is relatively long, deep posteriorly, but shallower toward the front. The opening into the incisive canal is slightly damaged, and there is some erosion of the opposing halves of the jaw just at the unfused midline. It appears as though the canal is centered about 10 mm behind the alveoli for the central incisor roots. Thus this structure is situated as in other African and Asian specimens. The canal follows an inclined path upward and rearward toward the nasal floor (Walker and Leakey, 1993). The rest of the palatal surface is generally smooth. Some small pits are filled with matrix, and there is a faint groove parallel to the cheek tooth row on the right side, but this juvenile individual exhibits less relief than can be documented for KNM-ER 3733.

#### NON-METRIC COMPARISONS

As detailed above, there is variation in facial morphology among the hominids examined. Anatomical similarities and contrasts are often summarized simply as lists of discrete traits, scored as present or absent (see below). However, such an approach will likely miss important information, relating to differences in character expression within groups. A more accurate (if less clear-cut) accounting can be conveyed first in narrative form.

#### Supraorbital region

The supraorbital tori of *H. erectus* are generally thickened, both centrally and toward their outer margins. Differences are evident, even when comparisons are restricted to the Asian specimens. The tori of Sangiran 17 resemble those of some Ngandong crania but are less strongly arched than is the rule at Zhoukoudian, and there is little supratatorial hollowing. The brow is continuously thickened in the Sangiran, Zhoukoudian, and Gongwangling people. In several of the Ngandong crania, it tends to be thinner centrally but relatively massive (forming a "trigone") at the lateral margin of each orbit. Causes of these differences are unclear. Sex dimorphism must play a role, but some of the variation is likely related to interpopulation changes in the way the face is "hafted" to the braincase. Facial forwardness and expansion of the sinuses, rather

than stresses generated by the teeth and jaws, seem to be principal determinants of supraorbital development (Hylander et al., 1991; Ravosa, 1991; Lieberman, 1995).

Among the African specimens, OH 9 is clearly a close match to Sangiran 17. The Olduvai cranium (probably a male) is large, and it possesses the massive tori and glabellar region associated with Asian *H. erectus*. The Koobi Fora individuals are smaller, and perhaps it is not surprising that the brow of KNM-ER 3733 is relatively gracile. In their analysis of Late Pleistocene and recent crania, Lahr and Wright (1996) demonstrate that superstructures including the supraorbital ridges are influenced by size (particularly glabella-occipital length and various facial breadths). It is likely that the same considerations apply to earlier *Homo*. In any case, where it can be measured on one side, the brow of KNM-ER 3883 is 11 mm thick centrally; a maximum reading is 13 mm. Contrasts between the African and Asian populations should not be overemphasized.

#### Nose and clivus

As described in Weidenreich's (1943) monograph, the nasal bones of *Sinanthropus* are broad in comparison to those of living humans and exhibit no narrowing below the nasal root. Superior breadth of the nose is substantial also for Gongwangling and for Sangiran 17, and in these specimens the bones are expanded inferiorly. Midline keeling is distinct. Combined width of the nasal bones is less for both of the Koobi Fora faces, and the proportions of the individual elements differ somewhat from the Asian condition. KNM-ER 3733 does display an internasal keel. The nose of the Nariokotome boy is very broad (equal in its dimensions to Zhoukoudian *H. erectus*), and the difference between superior and inferior widths is minor. In KNM-WT 15000 as for the other skulls in which this structure is preserved, the "crista nasalis" slopes forward to join the floor of the aperture in a relatively anterior position.

For the Zhoukoudian hominids, an anterior nasal spine is not developed. This is frequently the case for archaic *Homo*, and neither Gongwangling nor Sangiran 17 possesses more than a slight central protuberance. Among these Asian specimens, Sangi-



ran 4 stands apart. Here the incisive crest extends forward to produce an elevated process. For KNM-ER 3733, the area in question is partially eroded, but an anterior spine could not have been prominent. Much the same conclusion holds for the Nariokotome youth.

Cresting on the nasal sill is variable. The Gongwangling maxilla carries only faint transverse (spinal) crests, which do not reach the borders of the nose. The sill of Sangiran 17 is smooth. However, the corresponding region of Sangiran 4 shows more relief; spinal crests serve more clearly to separate the floor of the aperture from the subnasal surface below. KNM-ER 3733 displays the condition expected for *H. erectus*. The nasal surface is smooth anteriorly. In KNM-WT 15000, the sill is gutter-like to each side of the longitudinal incisive crest. It is marked only by faint transverse ridges that join the wall of the nose a few millimeters posterior to its anterior margin.

The junction between the posterior pole of the alveolar process and the hard palate can be observed in only three instances. This region is damaged for Sangiran 17, but it can be scored as smooth in Sangiran 4. For KNM-ER 3733, the topography of the floor is clearly stepped, but for KNM-WT 15000, it appears to be like that of the Asian specimen. Evidently this character, which shows little consistency within a sample of earlier *Homo* crania studied by McCollum et al. (1993), does not help to sort the hominids considered here.

The Zhoukoudian nasoalveolar clivus as depicted by Weidenreich (1943) is projecting and markedly convex in profile. This convexity is reduced in the new reconstruction prepared by Tattersall and Sawyer (1996), where the clivus appears more comparable to that of the Sangiran individuals. In the case of the Gongwangling maxilla, the subnasal surface seems to be flatter, and the canine jugum is quite well developed. This morphology converges on that of the African faces. In KNM-ER 3733, which like the Chinese specimens has been partially restored, the flat clivus is bounded by juga which reach upward, to thicken the lateral margin of the nose. This condition would probably be manifest also in the Narioko-

tome hominid, if the boy had matured a little further.

### Cheek region

Chinese *H. erectus* displays no canine fossa. Instead of generalized hollowing above the premolar roots, there is a narrow channel, trending upward toward the infraorbital foramen. Weidenreich (1943) terms this feature a "sulcus maxillaris," and likens it to a fold between the canine jugum and the zygomatic process. Traces of such a sulcus are preserved also for Gongwangling and Sangiran 17. Unfortunately, the face of KNM-ER 3733 is incomplete in this region, as is that of KNM-ER 3883. Neither specimen offers any indication that a canine fossa is developed. Although it is still shallow as a consequence of age, a sulcus fitting Weidenreich's description is clearly present in KNM-WT 15000. Evidently the African as well as the Asian hominids are plesiomorphic for this character.

Orientation of the zygomaticoalveolar crest is variable. Weidenreich's (1943) female shows a deep incisure, whereas the "male" cheek incorporated into the Tattersall and Sawyer (1996) reconstruction allows less curvature. For Sangiran 17, the pillar is approximately horizontal. Some flexion is apparent, but this is exaggerated in the reconstruction of Aziz et al. (1996). KNM-ER 3733 provides little information, but in KNM-WT 15000 the root of the maxillary zygomatic process is very thick. This crest curves laterally, so that an incisure is expressed.

Form of the cheek itself differs within both the Asian and the African assemblages. This part of the face is massive and rounded inferolaterally in the large male (?) from Sangiran but flatter in KNM-ER 3733. For KNM-ER 3883, just enough of the malar surface is intact to suggest substantial prominence and a contour similar to that of Sangiran 17. Whether the knob-like malar tubercle characteristic of the Zhoukoudian hominids occurs also in the Gongwangling material cannot be ascertained, but a tubercle is present in at least one of the Sangiran specimens. For KNM-ER 3733, the region in question is damaged, but traces of a tubercle survive. This structure seems

to project inferiorly, just at the zygomaxillary suture.

### Hard palate

The palate is partially or fully preserved in several cases. One important feature is the location of the opening to the incisive canal, described by Weidenreich as lying at a greater distance from the orale than is true of recent humans. This separation of the anterior wall of the canal from the incisor roots can be documented for the Sangiran as well as the Zhoukoudian specimens. In KNM-ER 3733 and in the Nariokotome boy, there is some erosion of the bone near the midline, but palatal morphology seems to match that of the Asian individuals. In these Kenyan examples, inclination of the axis of the canal is comparable to that in Chinese *H. erectus*, and there is no approach to the condition observed in later *H. sapiens*. Rugosity of the hard palate is clearly variable. The Zhoukoudian specimens exhibit ridges and appreciable pitting, whereas Sangiran 17 and especially Sangiran 4 have relatively smooth surfaces. KNM-ER 3733 and to a lesser extent KNM-WT 15000 tend to resemble the Chinese fossils.

### Variation and the utility of characters

States for 17 facial characters in 6 Asian and African assemblages are given in Table 2. Many of these traits are discussed by Weidenreich (1943) and later workers. Invariably there are differences of opinion as to how a given feature may be scored, but my definitions of characters and states generally follow those already established. Insofar as possible, measurements forming continuous distributions are avoided. Indices or angular values can be partitioned into "discrete" states, but this must always be done arbitrarily.

In practice, there is little constraint on the choice of characters to be utilized in sorting, and most regions of the face are represented in Table 2. However, it should be recognized that not all aspects of anatomy are equally useful for comparative purposes. Tobias (1991) provides a comprehensive discussion of questions surrounding the "taxonomic relevance" or "phyletic valence" of trait complexes, while Lieberman (1995) offers cau-

tionary notes on the selection of characters employed to infer evolutionary relationships. Care should be taken to ensure that such features are developmentally homologous across the groups considered. Especially where populations are closely related, the problem of convergence is likely to be serious. To minimize this difficulty, it is important to take growth mechanisms into account and to avoid structures heavily stressed by muscle/tendon attachment that may be modified by non-genetic factors during an individual's development. Given these constraints, it is possible to identify traits that are promising as indicators of affinity, in the sense that they are expressed consistently within groups and also show variation between species of Hominidae.

Although the contour described by the supraorbital tori (trait 1) is frequently emphasized in anatomical comparisons, this feature is clearly variable within assemblages of *Homo* fossils. Both the brow itself and the glabellar region are influenced in a complex way by facial forwardness and sinus development, and this part of the face is highly sexually dimorphic. Its utility for sorting at the species level is consequently lowered. Vertical thickness of the tori (trait 2) is consistently greater in the Asian groups than at Koobi Fora, but this feature is affected by cranial size (see above) and is again at least partly a reflection of sex differences. Nevertheless, a brow that is relatively "thin" at the center of the orbit is sometimes said to be diagnostic of the early African populations.

The nasal bones tend to be parallel-sided in specimens such as OH 24 (*H. habilis*) and KNM-ER 1470 (now often referred to *H. rudolfensis*). Nasal elements that are of approximately uniform width are found also in Asian *H. erectus* and in some groups of modern humans (Weidenreich, 1943), but this pattern contrasts with the condition observed in robust species of *Australopithecus*, where the bones are wide superiorly (Tobias, 1991). Nasal bone proportions (trait 4) thus offer some promise as an indicator of interspecific variation. Internasal keeling (trait 5) is present in (some) individuals of *Australopithecus* and early *Homo*, but whether a linear elevation restricted to the

TABLE 2. Characters and character states in the assemblages from China, Indonesia, and East Africa

Trait No.	Zhoukoudian	Gongwangling	Sangiran	Koobi Fora	Nariokotome	OH 9	Reference
1. Supraorbital torus, contour	Arched	Arched	Straight	Arched	—	Straight	Groves (1989) Rightmire (1990)
2. Supraorbital torus, vertical height	Thick	Thick	Thick	Thin	—	Thick	Groves (1989) Rightmire (1990)
3. Glabellar prominence	Variable	Indented	Projecting	Variable	—	Indented	
4. Nasal bone proportions	Uniform width	Uniform width (?)	Uniform width (?)	Narrow superiorly	Uniform width (?)	Constricted	Wood (1991)
5. Internasal keeling	Absent	Present	Present	Variable	Absent	Absent (?)	
6. Slope of "crista nasalis"	Forward	—	Forward	Forward	Forward	—	Weidenreich (1943)
7. Anterior nasal spine	Absent	Present (?)	Variable	Absent	Present (?)	—	
8. Nasal sill, anterior aspect	Smooth	Crested (?)	Variable	Smooth	Smooth	—	McCollum et al. (1993)
9. Nasal floor topography	—	—	Smooth (?)	Stepped	Smooth	—	McCollum et al. (1993)
10. Clivus profile	Convex	Flattened (?)	Convex	Flattened	Flattened	—	
11. Canine jugum	Strong	Strong	Weak	Strong	(?)	—	
12. "Sulcus maxillaris"	Present	Present (?)	Present	Present (?)	Present	—	Weidenreich (1943)
13. Malar surface, antero-lateral	Rounded	—	Rounded	Variable	(?)	—	Rak (1983)
14. Zygomaticoalveolar pillar	Flexed	—	Flexed	—	Flexed	—	Pope (1991)
15. Malar tubercle	Present	—	Present	Present	Absent	—	Pope (1991)
16. Incisive canal opening	Posterior	—	Posterior	Posterior	Posterior	—	
17. Palatal surface	Rugose	—	Smooth	Rugose	Smooth (?)	—	

suture line on an otherwise flattened bridge (as in OH 24) is developmentally comparable to the keeling produced where nasal elements are more sharply angled to one another (as in later *Homo*) is uncertain. The slope of the "crista nasalis" (trait 6) seems generally to distinguish earlier *Homo* from later humans.

McCollum et al. (1993) comment on the morphology of the subnasal region and confirm differences among species of *Australopithecus* in the position of the anterior attachment of the nasal septum, length of the sill, and topography of the nasal floor. However, these characters and others relating to crest development show considerable variation within a sample of early *Homo* crania. Table 2 suggests that expression of an anterior

spine (trait 7), cresting on the nasal sill (trait 8), and a smooth vs. stepped contour of the floor of the cavity (trait 9) also vary in *H. erectus*. For the Zhoukoudian hominids, Weidenreich (1943) describes the passage of the nasal floor onto the clivus as lacking either the crest or groove common in recent populations. This smooth condition is apparent in the African fossils, but at Sangiran and perhaps at Gongwangling, there is evidence of spinal cresting.

A buttress associated with the canine root and extending upward as an anterior pillar is present in the faces of many early hominids. This structure may form the medial margin of the maxillary sulcus. Such morphology is expressed in OH 24 and some other *H. habilis* as well as representatives of

*A. africanus* and *A. robustus* (Tobias, 1991). The canine buttress (trait 11) of Asian *H. erectus* is comparable to that of other groups but is less well developed superiorly, alongside the nose (Weidenreich, 1943). Probably a swollen jugum and the "sulcus maxillaris" (trait 12) should be regarded as primitive characters. Other taxa exhibit what seem to be derived morphologies. In *A. boisei*, the sulcus is filled out or obliterated (Rak, 1983), and in later *Homo*, this furrow is replaced by a hollowed canine fossa.

In *A. africanus*, the zygomaticoalveolar crest (trait 14) extends in a straight line obliquely from the body of the maxilla to the root of the zygomatic arch (Rak, 1983). In the robust australopithecines, the pillar is again straightened, and there is no curvature of its lower margin. Specimens of early *Homo* generally display a more horizontal (plesiomorphic?) orientation of the crest, and in OH 24, KNM-ER 1813, and SK 847 a notch (the malar incisure) is variably developed. Some flexion of the pillar is characteristic of most later *Homo*, although European Neanderthals show a relatively straight (apomorphic?) condition.

Trait 16 is also likely to be primitive for the groups compared in Table 2. The opening to the incisive canal is situated posteriorly on the Zhoukoudian palate, as noted by Weidenreich (1943). A similar placement is evident for *H. erectus* from other localities. Also, the canal is located relatively far posteriorly in the (very short) palates of OH 24 and KNM-ER 1813, and in the australopithecines. Only in later humans does the incisive canal come to lie in a forward position and assume a more vertical orientation within the jaw.

The foregoing suggests that traits relating to supraorbital development and glabellar prominence are problematical as indicators of affinity. Internasal keeling may be suspect on developmental grounds, while morphology of the nasal sill and floor is clearly variable within groups of *Homo*. The malar tubercle may also be of low utility, as this swelling is associated with the attachment of the masseter. Other characters seem generally to meet Lieberman's (1995) criteria, and these features show variation between taxa of Hominidae.

### Summary

Only a few characters from Table 2 serve to distinguish the Asian and African hominids. Brow thickness at Koobi Fora (but not Olduvai) is one example, but this trait is of low utility. Also, both of the Koobi Fora crania (but not the Nariokotome individual) have nasal bones that are narrow superiorly rather than uniformly wide. The clivus of KNM-ER 3733 is flattened in the transverse plane. In several of the Asian specimens, this surface is strongly convex, but it must be recognized that the Gongwangling clivus is intermediate in form. In many additional features, including some judged to be especially useful indicators of affinity, there is variation among individuals but no basis for sorting the fossils by geographic region. Still other traits such as the forward sloping "crista nasalis," the vertical furrow (Weidenreich's "sulcus maxillaris") below the infraorbital foramen, some curvature of the zygomaticoalveolar pillar, and the posterior location of the palatal opening into the incisive canal are present in all cases where the specimens are complete enough to be examined.

### MEASUREMENTS

Measurements taken on the more complete original specimens and the reconstruction of Skull XI from Zhoukoudian are provided in Table 3. Linear dimensions record heights and widths for the entire face and for its components treated separately. Several angles can be calculated, and one index used by Weidenreich is listed. Measurements of brow thickness confirm that there is variation in this feature, as noted previously. Supraorbital development need not be reconsidered here. In overall proportions of the facial skeleton, some further contrasts are evident. Upper facial heights do not vary by more than a few millimeters, but differences in breadth are greater. The biorbital diameter is consistently larger in the Asian faces than in the African specimens, and for the (rather massive) Gongwangling individual, this increase is especially pronounced. At the same time, projection of the nasal root relative to the lateral orbital margins is about equal in the Gongwangling

TABLE 3. Measurements of the more complete fossil faces from Zhoukoudian, Gongwangling, Sangiran, Koobi Fora, and Nariokotome

	Zhoukoudian <sup>1</sup>	Gongwangling	Sangiran 17	KNM-ER 3733	KNM-ER 3883	Nariokotome
Torus thickness, central	13.2?	15.0?	17.0	8.5	11.0	—
Torus thickness, lateral	—	—	13.0	9.0	7.0	9.0
Nasion-prosthion	77	—	>75?	81	—	77?
Biorbital chord	113	128?	114?	109	110	103
Nasion subtense	17	15?	20	12	14?	20
Nasion angle	147	154?	141?	155	151	138
Nasal bridge width	25	24?	24?	22	22	32
Nasal bridge height	7.5?	8.0?	9.0?	8.0	9.0?	9.5
Nasal bridge index	30.0	33.3	37.5	36.3	40.9	29.6
Nasal bridge angle	118	113	106	108	101	119
Orbit breadth	40	—	44	44?	45	39?
Orbit height	34	—	40	35	36	42?
Midorbital chord	—	—	66?	73	—	70
Naso-orbital subtense	—	—	18 <sup>2</sup>	15	—	19
Naso-orbital angle	—	—	123 <sup>2</sup>	135	—	123
Nasal breadth	30	—	29 <sup>2</sup>	36?	—	36
Nasal height	52.5	—	52.0?	53.0	—	57.0?
Clivus length	25	—	25?	30?	—	22
Bimaxillary chord	98?	—	116?	101	—	100
Subspinale subtense	24	—	30 <sup>2</sup>	17	—	22
Subspinale angle	128?	—	125?	143	—	133
Prosthion subtense	42?	—	—	41	—	40
Prosthion angle	99?	—	—	102	—	103
Cheek height	24	—	37	34	—	30
Maximum malar height	52?	—	57?	53?	>58?	53?
Palate breadth	40	—	—	—	—	40
Palate length	52	—	—	—	—	—

<sup>1</sup> Measurements for Zhoukoudian are taken on Skull XI as reconstructed by Weidenreich (1943).

<sup>2</sup> Measurement taken on the reconstruction of Sangiran 17 described by Aziz et al. (1996).

and Koobi Fora crania. As measured by the nasion angle, the frontal is flattened in the transverse plane. Values for this angle are somewhat lower (suggesting more protrusion in the midline) for both Sangiran 17 and the boy from Nariokotome, while the Zhoukoudian female is intermediate.

Width of the nasal bridge is comparable in the Zhoukoudian, Sangiran, and Koobi Fora individuals. The height/breadth index shows that the bridge is slightly flatter in Skull XI (30.0) than in Skull XII (for which Weidenreich gives a figure of 37.0). It is a little higher in KNM-ER 3883. Differences are not substantial, either in the index or the angle registering projection of nasion relative to the lacrimal crests. The broadest nasal region is that of KNM-WT 15000. The boy's bridge is also flattened, as both the index (29.6) and the angular reading (119°) are quite close to those for the Zhoukoudian adult.

The midorbital chord is a measure of maxillary breadth, taken at the inferior borders of the orbits. Because the necessary landmarks are not present in the Zhoukou-

dian reconstruction, this measurement cannot be obtained for Skull XI. For Sangiran 17, the chord is slightly reduced in comparison to those for the African crania. Elevation of the nasal saddle can be estimated from the reconstruction of Aziz et al. (1996), and the (naso-orbital) angle calculated from this subtense is the same for the Indonesian hominid as for KNM-WT 15000. The angle is greater for KNM-ER 3733, indicating that the saddle is lower. In this (damaged) Koobi Fora individual, the midfacial region is somewhat flattened.

### Ratio diagrams

Comparisons of this sort, intended to bring out shape differences among several specimens, are facilitated through the use of ratio diagrams. Such plots can be constructed for sets of measurements taken from Table 3. Nine dimensions of the upper face, nose, and orbits are displayed in Figure 3a. Here the horizontal scale records proportional differences among the fossils, relative to a single more complete cranium selected as a stan-



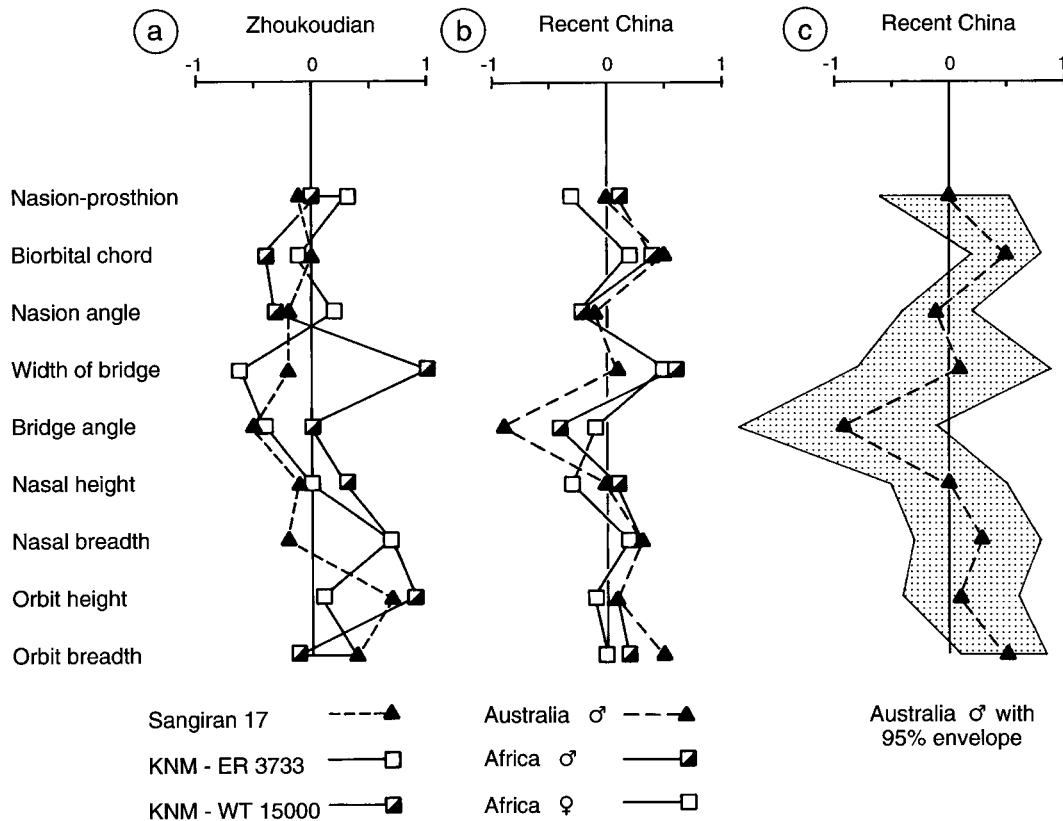


Fig. 3. Ratio diagrams constructed for nine measurements of the upper facial region. **a:** Skull XI from Zhoukoudian is taken as the standard against which other fossil crania from Asia and Africa are compared. Sangiran 17 departs from the standard in only minor ways, while the two Turkana hominids exhibit somewhat more marked proportional differences. **b:** Recent Chinese females constitute the standard, and modern Australians and Africans are compared on the same

battery of measurements. Here the horizontal scale gives proportional differences among the group means, relative to the Chinese average. **c:** The track for recent Australian males represents deviations of (log) mean values from the Chinese average. For each measurement, values corresponding to  $\pm 2$  S.D. from the (Australian) mean are also plotted, so as to construct an envelope within which about 95% of observations will lie.

dard. Despite some reservations about the accuracy of all of its features, Skull XI from Zhoukoudian is treated as the standard against which other Asian and African individuals are measured.

Several points emerge from consideration of the figure. First, log deviations from the zero axis are minor for Sangiran 17. For most of its dimensions, the Indonesian face is similar to or slightly smaller than that of the Zhoukoudian standard. The nasal bridge angle is especially reduced, but here the lower value reflects increased projection of the nasal root. Both height and width of the orbit are relatively large. For these last measurements, the track for Sangiran 17

suggests proportional changes relative to the Zhoukoudian female. The plot for KNM-ER 3733 is also roughly coincident with the zero axis, even if the nasal bridge is narrow superiorly, and the piriform aperture is relatively broad. KNM-WT 15000 seems to vary from the standard in these same features. In this individual, the nasal root is appreciably wider than that of Skull XI, as are both the nose and orbit. Which if any of these differences may be judged to be "significant" cannot be determined rigorously, but a general impression is that neither the Sangiran specimen nor the Koobi Fora adult departs greatly from the morphology displayed at Zhoukoudian. The Narioko-

tome face shows more proportional difference, perhaps because of its young age.

In Figure 3b, recent crania are compared on the same battery of measurements. Data are from Howells (1989). For consistency with the first diagram, a sample of Chinese females ( $N = 38$ ) is taken as the standard. Other populations considered are Australian males ( $N = 52$ ), East African males ( $N = 33$ ), and East African females ( $N = 50$ ). In this case, the horizontal scale gives proportional differences among the group means, relative to the Chinese female average. The Australian face differs from the standard in having greater biorbital breadth, a smaller bridge angle, and a somewhat larger orbit. African males generally follow the path of the Australians, while African females are a little smaller in most dimensions and more closely resemble the standard. Here the tracks for male crania do not precisely match those of Sangiran 17 in Figure 3a, but the pattern of prominence at nasion (reduced midline angles) and expanded orbital dimensions is similar. A reasonable interpretation is that the main differences between the Sangiran and Zhoukoudian specimens are consistent with those among males and females in living populations.

This plot based on mean values gives some information about facial variation in recent populations, but it conveys no clear sense of the limits expected for a species. In Figure 3c, Australian males are considered alone. As before, the track represents deviations of (log) mean values from the Chinese average. For each measurement, values corresponding to  $\pm 2$  S.D. from the (Australian) mean are also plotted, so as to construct an "envelope" within which about 95% of observations will lie. This envelope illustrates the dispersion expected for Australians (still relative to the Chinese standard). Treating the African population in the same way would expand the (intraspecific) limits for most variables. It is clear that the pattern obtained even for this geographically restricted sample of *H. sapiens* is comparable to that in Figure 3a. There is no indication that the fossils differ more than recent people, or that the variation observed among ancient Asians and Africans exceeds that within a single species.

For other parts of the face, variation is somewhat more pronounced. This is brought out in Figure 4a, constructed for seven measurements of the midface and cheek region. Sangiran 17 departs from the (Zhoukoudian) standard in bimaxillary breadth but not in prominence of subspinale. A much greater contrast is apparent in cheek height, and in fact the malar bone is relatively and absolutely massive in the Indonesian specimen. The two African crania differ from Skull XI in clivus length, but the deviations are opposite in sign. Both of these individuals have slightly increased angles at subspinale, registering flatness just below the nose. Cheek height is again proportionately greater than at Zhoukoudian. In this feature, the African faces approach but do not match the build of Sangiran 17. So, as with Figure 3, there is no clear separation of the Asian and African assemblages.

Figure 4b does suggest substantial departure of the recent human pattern from that of *H. erectus*. Here Zulu males ( $N = 40$ ) and females ( $N = 32$ ) from South Africa are plotted, relative to Zhoukoudian. In the modern face, clivus length is shortened. This change is accompanied by adjustments resulting in less projection of the alveolar process (an increased angle at prosthion) and less swollen canine juga. The malar region is relatively gracile. Cheek height is lower than that of Skull XI, and when the other fossils are considered, the contrast is still more striking. This reduction in malar massiveness (but not total height as measured to the zygomaticofrontal boundary) constitutes an important attribute of the midface in *H. sapiens*. Together with reshaping of the clivus, it must contribute to development of the canine fossa (a derived trait of the maxilla).

## DISCUSSION

Neither detailed anatomical comparisons nor the metric evidence just cited bring to light any consistent patterns in morphology which set the African hominids apart from Asian *H. erectus*. The Koobi Fora individuals have relatively gracile brows, but this may be a reflection of overall size and sex dimorphism. Also, the African faces tend to be high but less broad across the orbits than their Asian counterparts. Both of the Koobi

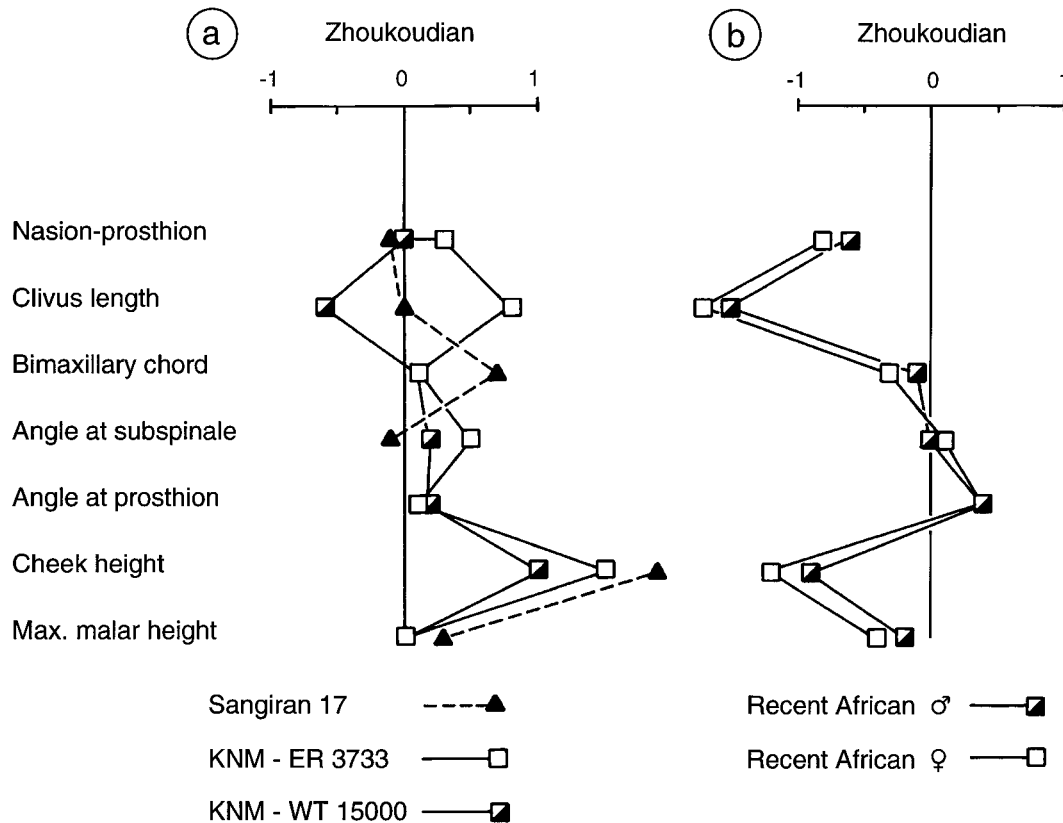


Fig. 4. Ratio diagrams constructed for seven measurements of facial height, the cheek, and the subnasal region. Skull XI is taken as the standard. **a:** Fossils from Sangiran and the Turkana Basin are compared to Zhoukoudian. Despite some contrasts, especially in cheek height, there is little indication that the African crania

can be separated from their Asian counterparts. **b:** Recent South African males and females are plotted, again relative to Zhoukoudian. In the modern face, clivus length is shortened. This change is accompanied by adjustments resulting in less projection of the alveolar process, and the malar region is relatively gracile.

Fora crania have nasal bones that are narrow superiorly, while the piriform aperture is relatively wide. In many other characters, including glabellar prominence, nasal bridge dimensions, internasal keeling, cresting on the nasal sill, topography of the floor of the nose, prominence of the canine jugum, orientation of the zygomaticoalveolar pillar, rounding of the anterolateral surface of the cheek, formation of a malar tubercle, and palatal rugosity, there is variation among individuals from localities within the major geographic provinces. Some of these traits are likely to be of low taxonomic utility, but even for those judged to be important indicators of interspecific variation, it is not possible to identify states that are unique to either the Asian or African assemblages.

Additional features such as a forward sloping "crista nasalis," presence of a "sulcus maxillaris," a high (and massive) cheek coupled with some flexion of the malar pillar, and a posterior position of the incisive canal are present in all groups. These characters seem to be plesiomorphic, in comparison to the derived states evolved in later humans.

If the differences in supraorbital development and nasal breadth are not granted special significance, then much or all of the variation in form of the upper face and orbits, nose, cheek, and palate can be attributed to sex dimorphism and/or local differentiation of populations within the Asian and African geographic regions. This interpretation is strengthened by the ratio diagrams of

Figures 3 and 4. Changes in nasal bridge projection and orbit size distinguishing Sangiran 17 from Zhoukoudian Skull XI are similar to those separating recent males from females. Contrasts between the Asian and African faces are perhaps less easily attributed to sex alone, although Sangiran 17 is almost certainly male, while KNM-ER 3733 is likely to be female. In any case, the patterns of Figure 3a, c suggest that variation among the fossils is comparable to that observed in a subset of recent *H. sapiens*. There is no evidence that the Pleistocene hominids show greater dispersion than expected within the confines of a single species.

This finding is difficult to reconcile with the work of Bilsborough and Wood (1988), who have undertaken a comprehensive analysis of facial dimensions in early hominids. In their multivariate study, Bilsborough and Wood determine that early African "*erectus*" is 9.7  $D^2$  units from late *H. erectus* at Zhoukoudian. This separation is of the same order as that between Neanderthals and modern *H. sapiens*. However, the significance to be attached to this distance is uncertain. The same analysis places late *H. erectus* closer (6.4 units) to recent humans, although it is clear that one of the authors has come to view the Asian hominids as distinctive morphologically and therefore "peripheral to the main . . . locus of human evolutionary change" (Wood, 1994). Despite its greater distance from modern populations, African "*erectus*" is in fact held to be more closely related to *H. sapiens*. Apparently the  $D^2$  results, affected by small sample size, are inconsistent with conclusions reached by other methods. The assessment of Bilsborough and Wood (1988) is based only on KNM-ER 3733 and Weidenreich's Zhoukoudian reconstruction. Their finding must be tempered by the fact that measurements taken on a larger suite of individuals (Table 3) do not offer grounds for distinguishing two taxa.

The facial evidence presented here is generally in keeping with observations made on other parts of the cranium, lower jaw, and teeth. Specimens from the Turkana Basin, Olduvai Gorge, and other sites in Ethiopia and northwestern Africa exhibit essentially

the same set of traits as do those from the Far East (Rightmire, 1990). When KNM-ER 3733 is compared to an Asian cranium of comparable size, overall proportions are remarkably similar, as are many details in the construction of the temporomandibular joint, the tympanic plate, and mastoid region. Vault thickness as measured near the junction of the frontal and parietal bones is about the same in the East African and Asian samples (Walker, 1993). Also, the teeth from Koobi Fora and Nariokotome are close in size and shape to those from Zhoukoudian (Brown, 1994). Certainly there are not many traits that can be used to distinguish the Turkana fossils as a separate species, and I will argue that the names *H. ergaster* and/or *H. leakeyi* are unnecessary.

### Species definitions

The nature of "species" has been much debated, both by biologists working with living organisms and by paleontologists who confine their efforts to examining the fossil record. This extensive literature need not be reviewed in detail. However, in any discussion focusing on how taxa within *Homo* are to be recognized, it is important to be clear about the more general question of species definitions. In my view, species are "real" entities rather than artificial constructs. A species is a reproductive community, structured by the ability of its members to interbreed and bounded in the sense that genes are not exchanged beyond the group. Put another way, as by Paterson (1985), members of a species share a specific mate-recognition system, which can be studied in living animals and (sometimes) identified in fossilized remains (Turner, 1985; Masters and Rayner, 1996). Seen in this light, species may be broken up into local populations, and they can accumulate phenotypic change through time. However, they are still discrete entities with individual life histories, and they are inevitably subject to extinction. The question of whether such lineages can or should be subdivided in the manner proposed by Simpson (1961) is contentious. Of course, successive "chronospecies" have been described by paleontologists and anthropologists (for review see Gingerich, 1985), but my own feeling is that such taxa must

(always) be defined arbitrarily, by changes in morphology or stratigraphic breaks (gaps in the record). As noted by various workers including Eldredge (1993), these groups are not discrete species in the sense outlined above. Their utility as grades remains uncertain.

If the concept of species as evolutionary lineages is accepted, then several formal definitions may be entertained. One is that of Wiley (1978), who has extended Simpson's work but is careful to observe that lineages should not be subdivided. No matter how much morphological change may be apparent within a sequence of reproductively linked populations, no separation of ancestral and descendant "species" is permissible. This relatively broad concept, difficult to apply, differs from others which hold that non-reproductive features may provide a legitimate basis for defining subgroups. Here the issue is the level at which differentiation within a species as defined by Paterson (1985) may produce entities that are discrete, in the sense that they will not be subject to dissolution by virtue of a shared mate-recognition system (Eldredge, 1993). Cracraft (1987, 1989) suggests that a species is "an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." As defined in this way ("phylogenetically"), species are considered to be the smallest complete lineages among which there is a hierarchical pattern of relationships. Given its emphasis on criteria associated with ancestry (diagnostic characters indicative of reproductive cohesion), the phylogenetic concept has gained substantial support among paleontologists (e.g., Kimbel and Rak, 1993). However, the question of how diagnosable a population must be to qualify for species rank is problematical.

### Conclusion

No matter how these questions are resolved, it seems clear that the Asian and African assemblages treated here are very similar. In relation to the hominids from Java and China, the Turkana Basin specimens are not "diagnosably distinct," and it is difficult to find any basis for referring the

African fossils to a separate species. All of these populations can be placed in *H. erectus*. Although its phylogenetic origins remain obscure, this lineage must be rooted in Africa. Material from Koobi Fora including the cranium of KNM-ER 3733, other less complete crania, lower jaws, and the partial skeleton numbered KNM-ER 1808 are 1.8 to 1.7 Myr old. Fragments such as the KNM-ER 2598 occiput (perhaps belonging to the same taxon and found below the KBS Tuff) are still more ancient (Feibel et al., 1989). There is as yet no confirmation of any greater age for fossils from Asia (as claimed by Huang et al., 1995). It has been assumed that movement of populations out of Africa into other regions began well before 1.0 Myr ago, and new radiometric dates now suggest that the oldest Indonesian localities may be 1.8 to 1.6 Myr in age (Swisher et al., 1994). If these results can be verified, it will look as though *H. erectus* spread quite rapidly into the East Asian tropics. The species then flourished for a long time. At sites such as Zhoukoudian and Longtandong (Hexian) in China, *H. erectus* is known from deposits of the later Middle Pleistocene, while at Ngandong in Indonesia, at least one group of archaic people seems to have survived even into the Late Pleistocene (Swisher et al., 1996). These Ngandong hominids may document the last appearance of the lineage.

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